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Report

Canopy Flow Analysis Reveals the Advantage of Size in the Oldest Communities of Multicellular Eukaryotes

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Summary

At Mistaken Point, Newfoundland, Canada, rangeomorph "fronds" dominate the earliest (579–565 million years ago) fossil communities of large (0.1 to 2 m height) multicellular benthic eukaryotes. They lived in low-flow environments, fueled by uptake [1–3] of dissolved reactants (osmotrophy). However, prokaryotes are effective osmotrophs, and the advantage of taller eukaryotic osmotrophs in this deep-water community context has not been addressed. We reconstructed flow-velocity profiles and vertical mixing using canopy flow models appropriate to the densities of the observed communities. Further modeling of processes at organismal surfaces documents increasing uptake with height in the community as a function of thinning of the diffusive boundary layer with increased velocity. The velocity profile, produced by canopy flow in the community, generates this advantage of upward growth. Alternative models of upward growth advantage based on redox/resource gradients fail, given the efficiency of vertical mixing. In benthic communities of osmotrophs of sufficient density, access to flow in low-flow settings provides an advantage to taller architecture, providing a selectional driver for communities of tall eukaryotes in contexts where phototropism cannot contribute to upward growth. These Ediacaran deep-sea fossils were preserved during the increasing oxygenation prior to the Cambrian radiation of animals and likely represent an important phase in the ecological and evolutionary transition to more complex eukaryotic forms.

Results and Discussion

Flow and the Rangeomorph Community

Ediacaran-age rangeomorphs form the oldest known communities of eukaryotes. The large surface area of rangeomorphs, generated by self-similar fractal branching [1] (Figure 1), supports osmotic uptake [2, 3] as their nutritional mode. However, prokaryotes appear to have a kinetic advantage over eukaryotes in surface uptake of dissolved metabolites [4–6]. Here, we explore the potential benefit of eukaryotic height in low-flow deep-water benthic osmotrophic communities where bacterial uptake is constrained by size.

Even at comparatively low flow speeds and over relatively smooth sedimentary surfaces, the benthic boundary layer is turbulent. Within the benthic boundary layer, immediately above the bed, there is a thin region (the diffusive boundary layer, DBL) where mass transport is governed by rates of molecular diffusion, which are far slower than turbulent rates of mixing. Benthic bacteria in reducing deep-water environments today often form elongated sheaths or employ motility to escape limits imposed by diffusion in the submillimeter DBL near the sediment/water interface [7, 8]. However, limits on cell size and multicellularity in prokaryotes constrain their ability to extend further off the seafloor. In contrast, multicellular eukaryotic architecture permits much greater extension off the bottom. Thus, if substantial velocity gradients were to extend far off the seafloor, a significant advantage for osmotrophic organisms of larger size might then be anticipated.

Remarkable bedding-plane preservation at Mistaken Point, Newfoundland, Canada permits reconstruction of height, shape, and spacing of the individuals in these communities of Ediacaran age, while the sedimentology permits paleoenvironmental reconstruction [9, 10]. Fine-grained, laminated mudstones of the fossiliferous strata were deposited on the tops of turbidites and preserved below ash falls. They lack sedimentary structure or winnowing [10], indicating low near-bottom flow velocities (1–5 cm/s). A reductant-rich deep ocean [11, 12] potentially containing significant concentrations of dissolved or particulate organic carbon, ferrous iron, and hydrogen sulfide gave way to a more oxygenated deeper ocean later in the Ediacaran [12], a time interval captured by deposition at Mistaken Point ([13]; see "Ediacaran Oceanography" in the Supplemental Experimental Procedures available online). This habitat existed below the photic zone in a deep-water turbidite basin, precluding photosynthesis [10, 13]. The deep-water environment, combined with the co-occurrence of reduced compounds as well as oxygen, supports the osmotrophic interpretation for the rangeomorph community. Detailed understanding of fossil form and distribution, combined with an understanding of the flow regime derived from sedimentology, permits comprehensive modeling of the hydrologic and diffusive processes operating in the community.

We reconstructed flow in several rangeomorph fossil communities based on detailed quantification of fossils on bedding planes [14, 15] (Figures 2A, 2B, and S1). Canopy flow models, appropriate to the density and size of fossils observed in Mistaken Point communities, were used to reconstruct

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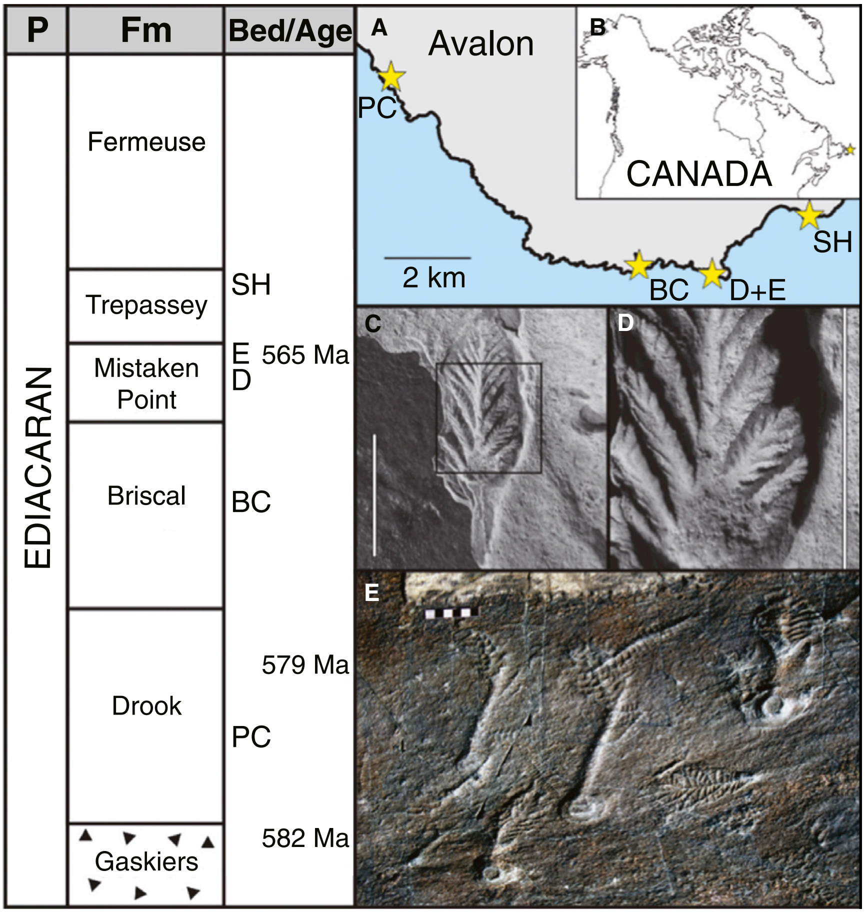

Figure 1. Overview of Stratigraphy, Preservation, and Morphology of Rangeomorphs

The stratigraphic column of Ediacaran localities with radiometric ages from Mistaken Point, Newfoundland, Canada is shown at left.

(A and B) Coastline from southeastern Avalon Peninsula in Newfoundland, with yellow stars representing specific beds studied.

(C and D) *Avalofractus abaculus* showing modular rangeomorph construction (C), with self-similar, repeatedly branched rangeomorph frondlets suggestive of osmotrophy (D) [1]. Scale bars represent 1 cm (C) and 0.5 cm (D).

(E) Ediacaran bedding surface (“E surface”) showing elements of a complex community preserved on a bedding plane; in this case, larger forms with holdfasts are *Charniodiscus*, with lower-tier *Fractofusus* and upper-tier *Beothukis*. Scale bar represents 5 cm.

velocity, vertical mixing, and organismal uptake as a function of height in the paleocommunities. This suite of analyses demonstrates how the structure of flow in benthic osmotrophic communities provided a selective advantage to eukaryotes extending off the ocean floor at the scale (0.1 to 2 m) observed. Furthermore, these analyses allow us to exclude other plausible adaptive scenarios in which large osmotrophs benefit from limited mixing of metabolites on the scale of the community (Figure S3).

The Canopy Flow Model

Rangeomorph communities constitute relatively dense arrays of vertical elements extending into the flow. Sufficiently dense arrays (or “canopies”) engender “canopy flow,” a flow regime distinctly different from turbulent boundary layer flow. Canopy flow is characterized by Kelvin-Helmholtz (KH)-type instability, which produces a “street” of coherent vortices in the flow [16, 17]. Such vortices form at the interface between flows of similar direction and differing velocity [18], as occurs at the top of a canopy, and dominate the mixing of mass and momentum across the interface [16, 19]. Consequently, the structure of canopy flow is quite distinct from that of turbulent boundary layer flow. In particular, vertical gradients of velocity and rates of vertical mixing at the top of the array or community, critical in understanding the impetus for rangeomorph growth, are both enhanced in canopy flow [20]. Thus, it is important to determine vertical profiles of velocity and mixing using the canopy flow framework. For a canopy flow modeling framework to be appropriate, the community must be sufficiently dense; C_Dah, a function of the canopy drag coefficient (C_D), frontal area per unit volume (a), and height (h), provides an appropriate measure of density [21–23]. Above $C_Dah = 0.1$, vortices are generated and the canopy flow framework pertains. The density of the community studied here (Mistaken Point bed D, $C_Dah = 0.21$) warrants canopy flow analysis. Additional criteria for application of the canopy flow framework relating to the flow velocity and organism stiffness also apply here. See Supplemental Experimental Procedures for details regarding the application of the canopy flow method to rangeomorph communities and consideration of increasing community density and height during community succession.

Flow Results

We present detailed modeling for a 1 cm/s flow over bedding plane D at Mistaken Point in Figure 2. Fossils were approximated as simple geometric forms, permitting calculation of a (frontal area) from height and width measurements. Calculations with higher velocities produce curves of identical form, and reconstruction of other bedding surfaces produces similar results (Figure S1). Contributions of different genera in the community were determined (Figure 2B), as well as vertical profiles of velocity (Figure 2C) and vertical diffusivity, a measure of mixing (Figure S1). These results show that flow velocities are reduced in the presence of the community (Figure 2B) whereas vertical mixing is increased, elevating rates of mixing through the community to the sea floor. This increased mixing results from the generation of KH vortices produced in canopy flows.

Determination of Uptake

Uptake by the community is controlled by two factors: diffusion across the DBL near the organismal surface, which is strongly impacted by the local velocity, and transport across the biological surface. To quantify active transport, we employ a surface transport parameter k with units of velocity (see Supplemental Experimental Procedures). The vertical velocity profile through this community reveals that growth off the seafloor exposed

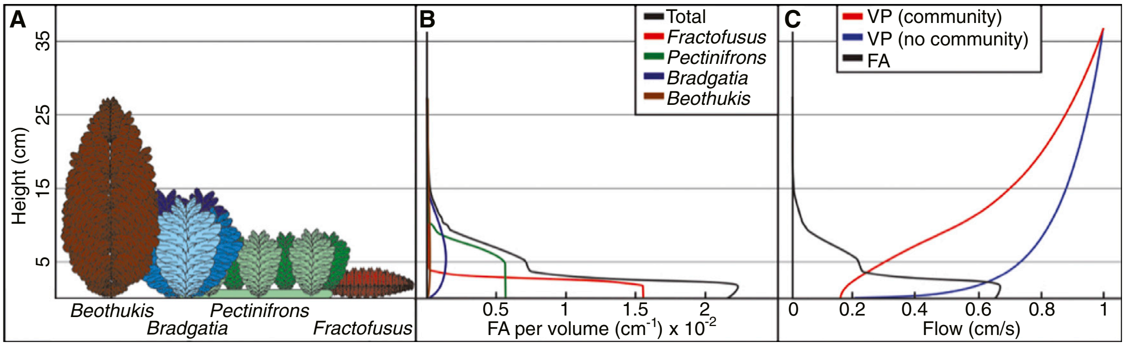

Figure 2. Velocity Profile Reconstruction, Mistaken Point Bed D

(A) Height of primary taxonomic components that make up the community.

(B) Frontal area per unit volume (FA) versus height above the sediment surface by taxonomic contribution and as a total. *Fractofusus* dominates a low (<4 cm) tier, *Pectinifrons* and *Bradgatia* dominate a middle (4–15 cm) tier, and *Beothukis* and other taxa form a high (>15 cm) "frond" tier.

(C) Modeled velocity profiles (VP); note the dramatic reduction in velocity in the presence of the community relative to a smooth surface. See also Figure S1.

rangeomorphs to increasing flow in an otherwise low-velocity setting (Figure 2C). In this low-velocity regime, exposure to higher flow overcomes limits imposed by the submillimeter DBL at the organismal surface (Figure 3), dramatically increasing the potential for metabolite uptake. In the parameter space likely to be operative in the community (based on known surface transport rates at comparable biological surfaces and the relevant local velocities within the community of order 1 cm/s or less), changes in flow velocity will contribute more substantially to change in uptake than will comparable changes in the kinetics at the organism's surface. Furthermore, if one assumes a particular surface transport rate (*k*) for the rangeomorph organisms, the uptake rate at any given height in the community can be determined (Figure 4B) on the basis of the velocity profile in the community (Figure 4A). The advantage of upward growth, as determined by the increase in uptake of a slightly taller organism (or growing tip), is then determined by the slope (derivative) of the uptake curve relative to height (Figure 4C). This exercise illustrates the dramatic advantage of upward growth in the community. This effect is substantial over a wide range of heights (Figure 4C), encompassing the growing tips throughout much of the community (Figure 2A). The ratio of uptake gradients between the canopy flow in the community and the boundary layer flow generated in the absence of a dense community (Figure 4C) shows that the community provides an upward impetus to growth at all heights above approximately 1 cm. Thus, upward growth of the community appears to be in significant part a response to the structure of the flow generated by the dense community itself.

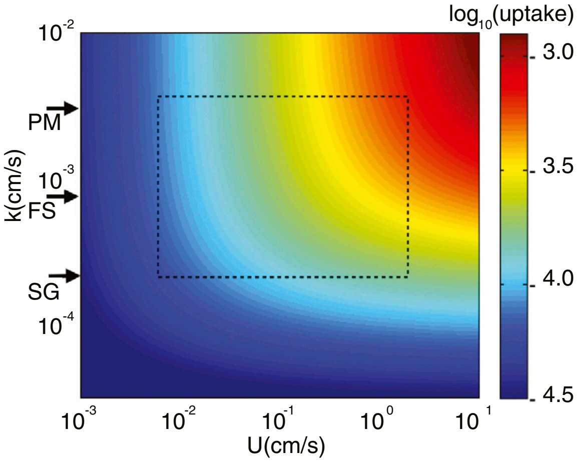

Figure 3. Surface Uptake as a Function of Local Velocity and Organismal Surface Transport

Surface uptake rate (per unit of surface area per unit of concentration outside the diffusive boundary layer [DBL], in cm/s) as a function of local flow velocity (*U*) and a surface/membrane transport parameter (*k*). At lower velocities, diffusion across the DBL is limiting, and any change in local velocity impacts the diffusive boundary layer controlling the amount of uptake. Higher velocities remove diffusive limits to uptake, and organismal transport (*k*) limits uptake. Values of *k* determined for a prokaryotic mat "PM," frog skin "FS," and seagrass "SG" are shown (see Figure S2 for determination). Horizontal contours of uptake (lower right) indicate uptake controlled exclusively by the transport parameter *k*. Vertical contours of uptake indicate that velocity completely controls uptake. In the region of interest likely to characterize flow within the rangeomorph communities [dashed box: $U \leq$ O(1 cm/s) and $k \sim$ O(10^{-3}–10^{-4} cm/s)], organismal uptake is more sensitive to a difference in velocity (*U*) than to differences in the active transport rate (*k*) at the surface of the organism.

Rejection of Alternative Explanations

From this work, exposure to flow is revealed as a critical aspect of osmotrophic nutrition within a fossil rangeomorph community, yielding the novel interpretation that growth in rangeomorph eukaryotes likely resulted from, and responded to, selection and competition for access to flow. Given the flow structure within the community (Figure 2C), vertical growth exposes the individual organism to higher local velocities, which are clearly advantageous in terms of uptake across the boundary layer at the organismal surface (Figures 3 and 4C). Other potential explanations for an advantage of height in an osmotrophic community involving concentration gradients (Figure S3) initially appear realistic but can be eliminated from consideration, as modeling reveals enhanced (not diminished) vertical mixing in the presence of the community. KH vortices generated at the canopy (Figure S1) produce this mixing. Given this mixing, uptake at organismal surfaces or the release of reactants from the benthic DBL cannot significantly alter concentrations within the community (Figure S2). Consequently, community density per se does not negatively impact osmotrophic function, confirming the importance of velocity access in adaptive response and access to velocity as a significant source of competition in these community settings.

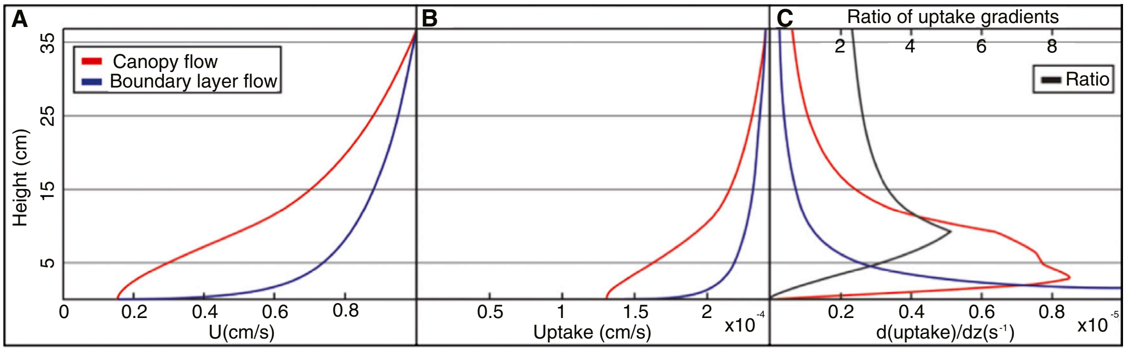

Figure 4. Uptake as a Function of Height Off the Bottom in the Rangeomorph Community

(A) Increase in velocity with height for the canopy flow produced by the community modeled (red) and a boundary layer flow (blue) generated in the absence of a dense community, as in Figure 2C.

(B) Increase in uptake (per unit of surface area per unit of concentration, in cm/s) with height above the bottom, for $k = 1 \times 10^{-3}$ cm/s.

(C) Vertical gradients of potential uptake in the flow. This indicates the adaptive growth advantage of increased height. There is a much greater adaptive impetus to grow to larger size in a canopy flow due to the stronger velocity gradients at the top of the community (see also Figures S3 and S4). The ratio of the two models (black line) is also plotted. This ratio serves to show that, with the exception of a thin region near the bed, the modification of flow produced by the community is responsible for a dramatic upward growth advantage that is not present in an unencumbered flow (see also Figure S4).

Community Variation and Succession

Not all rangeomorph communities are as dense as the one modeled here (Figure S1). Additionally, following turbidite deposition or ash fall (dramatic events that form the sedimentary bedding surfaces), community succession must have occurred. Presumably, surficial bacterial mats of some roughness, such as those produced by *Beggiatoa* in modern deep-sea environments, would represent an initial stage of the benthic community. Successive recruitment and growth of rangeomorphs of increasing height and density would then follow [14, 15]. With initial relatively smooth conditions (Figure 4A; blue curve represents boundary layer flow), velocity gradients will be steepest close to the seafloor. Thus, an initial impetus to grow up off the ocean bottom will be present (Figure 4C), and any increment of growth will yield substantial increase in velocity exposure. This initial condition is very much the situation encountered by bacteria in the deep sea today [7, 8]. Subsequent growth of rangeomorphs would then generate a transition to canopy flow as community density increased with upward growth (Figure 4; see also Supplemental Experimental Procedures for further discussion).

Our results have a number of implications for the Ediacaran fauna. It is likely that competition between rangeomorphs for exposure to flow was operative in the communities preserved at Mistaken Point, and it may be involved in the tiering observed there [14, 15, 24] (Figures 1 and 2A). The presumptive sponge *Thectardis* [25] is found at a low tier in the Mistaken Point community, where flows are minimal. Such low flow may have advantaged the active pumping of sponges relative to rangeomorphs, presumed to passively interact with flow. As noted above, *Beggiatoa*-like bacterial mats are modern osmotrophic communities [8] that push the limits on size and multicellularity in prokaryotes. Elephant-skin texture on Ediacaran bedding surfaces likely represents preservation of similar rough mats [26]. These textures tend to co-occur with rangeomorphs [27] and presumably reflect the presence of redox conditions suitable for osmotrophy. Such mats presumably formed the lowest prokaryotic tier in Mistaken Point-type communities. A detailed understanding of niche partitioning and tiering involving flow is a subject for future investigation. Flat-lying nonrangeomorph Ediacaran fossil forms from other localities appear later in the rock record [28] in coarser sediments that suggest substantially higher flow velocities and are characterized by sedimentary structures indicative of shallower-water settings within the photic zone. If these are also osmotrophs, they are pursuing that mode of life in a distinctly different way.

More generally, multicellular eukaryotes presumably evolved with some degree of independence in multiple lineages [29], and scenarios of multicellular adaptive advantage have been advanced for other eukaryotic lineages. These include dispersal of propagules, phototropism, and limiting dislodgement [30]. With a few exceptions, such as examination of locomotion and resource acquisition in *Volvox* colonies [31], functional assessments of the selective advantage of the multicellular condition have not been performed, and none of these assessments have involved the paleoreconstruction of the selective environment as has been done here. The size advantage of multicellular eukaryotes in osmotrophy at the time of Ediacaran deep-water oxygenation has implications for the radiation of animals. Regardless of the exact relationship between rangeomorphs and animals, the evolution of large multicellular osmotrophs in response to flow preceded and set the ecological stage for the ensuing evolutionary radiation of animals in the late Ediacaran and Cambrian [32, 33].

Other Applications

Canopy flow approaches similar to that employed here should also be fruitful in modeling a wide range of phenomena, including aspects of crystal or stromatolite growth [34], as well as uptake or particle capture in paleocommunities, such as that found in the filter feeding and tiering in crinoid communities [35]. Such models may also find a wide range of applications in modern biological contexts, including the assessment of nutrition in deep-water corals that could have some similarities to the rangeomorph communities addressed here [36].

Conclusion

Given the premise of osmotrophic nutrition of the Mistaken Point rangeomorphs, reconstruction of flow in dense communities leads to the interpretation that there was a selective advantage to large size related to access to flow. Higher flow across surfaces of taller forms permitted more rapid uptake, conferring an advantage to larger eukaryotes relative to prokaryotes. Competition between rangeomorphs also likely played a role in structuring the community. More generally, our results suggest that large multicellular benthic forms initially evolved in the Ediacaran in response to this size-selective advantage at a time when deep waters were transitioning to a more oxic state. This oxidative transition is thought to be particularly conducive to osmotrophy. Thus, this combination of factors, including selection for large size in osmotrophs exposed to low flow, appears to have precipitated a transition to larger eukaryotic forms that was followed rapidly by the evolution of motile heterotrophic animals.

Supplemental Information

Supplemental Information includes four figures and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2013.12.017.

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